

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

Islands in cities: urbanization and fragmentation drive taxonomic and functional variation in ground arthropods

This is the author's manuscript

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1723130> since 2023-01-27T10:20:43Z

Published version:

DOI:10.1016/j.baae.2020.02.001

Terms of use:

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)

Islands in cities: urbanization and fragmentation drive taxonomic and functional variation in ground arthropods

Elena Piano, Davide Giuliano, Marco Isaia*

Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123 Turin, Italy

*Corresponding author. Tel: +390117604544

E-mail address: marco.isaia@unito.it

Abstract

The conversion of natural lands in urban areas is exponentially increasing worldwide, causing a major decline in biodiversity. Environmental alterations caused by urbanization, such as land conversion and isolation of natural patches, favour tolerant and generalist species, causing both species loss and replacement. In addition, selective pressure is exerted on particular functional traits, driving a functional homogenization or turnover of biotic communities. We sampled ground arthropods within the municipality of Turin (NW-Italy), wherein an isolated and a connected control subplot were repeatedly sampled at 15 stations distributed along a gradient of increasing urbanization. Such a nested sampling design allowed us to investigate the taxonomic and the functional responses of carabids and spiders to both the urbanization level and patch isolation. First, we highlighted the dominant role played by species homogenization (*nestedness*) in explaining both taxonomic and functional variation in both groups of arthropods. Secondly, we showed that urbanization causes simultaneously functional homogenization and replacement in both carabid and spider assemblages, whereas patch isolation influences carabid species composition and homogenizes and shifts spider taxonomic and functional composition. Lastly, by relating community-weighted means of body length, dispersal capacity and trophic strategy to the urbanization and isolation gradients, we demonstrated that urbanization alters the trophic structure of both taxonomic groups and increases the average dispersal capacity of spiders. On the other hand, patch isolation affected the

functional composition of spiders only, reducing the body size and increasing dispersal capacity and the proportion of web-builder species. Our results demonstrate that both urbanization and patch isolation alter species composition by causing functional and taxonomic homogenization. In addition, they exert a strong filtering effect on community functional traits, increasing the proportion of phytophagous species in carabids, and increasing dispersal capacity and web-builders occurrence in spiders, while reducing spider body size.

Keywords: taxonomic homogenization; functional homogenization; carabids; spiders; traits

Introduction

Throughout recent human history, the conversion of natural lands in urban areas increased exponentially everywhere in the world (Seto et al., 2011), representing today one of the main anthropogenic impacts on natural ecosystems (Grimm et al., 2006). In particular, the process of urbanization induces major detrimental effects on the environment, as a result of the severe and fast changes in landscape structure and physical conditions (Parris, 2016). These alterations are common to all urban settlements, and they are expected to drastically affect biodiversity in all continents (McKinney, 2006). However, although an increasing number of studies investigated the relationship between urbanization and species richness, the underlying mechanisms that drive biodiversity patterns in urban areas are not fully understood (but see Shochat et al., 2006, 2010; Pickett et al., 2011; Turrini & Knop, 2015), with inconsistent results among the studied taxa (see Chace & Walsh, 2006; McKinney, 2008; Niemela & Kotze, 2009; Luck & Smallbone, 2010; Jones & Leather, 2012; Ramirez-Restrepo & MacGregor-Fors, 2017; Piano et al., 2019).

From an evolutionary point of view, urbanization represents a primary selective pressure on biotic communities, especially when considering the hindrance to the establishment and/or survival of certain species (McKinney, 2002). Such a strong environmental filter is expected to differentially affect species from the regional pool, by either favouring tolerant taxa or disfavouring the most sensitive ones, with subsequent changes in species composition, mostly due to species loss (Sadler et al., 2006; Magura et al., 2008; Niemelä & Kotze, 2009; Piano et al., 2017) or to species replacement (Sattler et al., 2010; Vergnes et al., 2014; Knop, 2016) along the urbanization gradients. As a result, both phenomena result in biotic homogenization, due to the loss of rare and specialised species, and the gain of widespread tolerant ones (McKinney, 2006).

In this context, a prerequisite to properly describe the mechanisms that drive variations in taxonomic and functional community composition (β -diversity) is the evaluation of the relative contribution of *turnover* and *nestedness*, whereby *turnover* measures the degree to which species are replaced by others—species replacement—and *nestedness* measures the degree to which communities of species-poor sites are a subset of those in species-rich sites—i.e. species loss (Ulrich, Almeida-Neto & Gotelli, 2009). To our

knowledge, this approach has never been applied to investigate ground arthropod communities in urban areas (but see Brice, Pellerin & Poulin, 2017 and Gianuca et al., 2017 as examples in other contexts).

According to the “habitat templet theory” (Southwood, 1977, 1988), the above-mentioned selection process may have major effects on particular functional traits, like morphological or physiological attributes, or it could affect the realized niche of a certain species (Webb et al., 2010). Interestingly, several studies confirmed this hypothesis, providing evidence that, by filtering species according to their life-history traits and ecological needs, urbanization often determines shifts in life-history community traits, i.e. functional replacement (e.g. Vergnes et al., 2014; Concepción et al., 2015; Gianuca et al., 2017; Merckx et al., 2018), or deletions of some functional groups, i.e. functional loss (e.g. La Sorte et al., 2014; Piano et al., 2017). As a consequence, urbanization may favour species with common traits conferring positive fitness under local conditions, causing the overall functional homogenization of urban communities (Olden et al., 2004).

The study of urban-rural gradients has been successfully used to highlight the effects of urbanization on biotic communities (McDonnell & Hahs, 2008). However, urbanization gradients are indirect and complex, since they include different types of disturbance acting at different spatial scales (Pickett et al., 2011; Parris, 2016), and changes in community may depend on several factors associated with urbanization (Rebele, 1994; Seto et al., 2011). For instance, urbanization correlates with a higher presence of impervious surfaces, which are known to have an effect on temperature, soil nutrient cycling and gas exchange and other physical or chemical parameters (Parris, 2016). In addition, the growth of urban areas is responsible for natural and semi-natural habitat fragmentation, which creates small and isolated residual patches, which are typically highly dynamic and impermanent ecosystems (Parris, 2016). Accordingly, since physical and landscape alterations are strongly correlated, even acting synergistically along urbanization gradients with similar demographic consequences, it is often difficult to distinguish their effects on biotic communities. Therefore, in order to isolate and describe their effects on biodiversity, a hierarchical approach is required, taking into consideration the nested nature of ecological systems (McDonnell & Hahs, 2008).

In this research, we aimed to assess which mechanisms are involved in shaping ground arthropod assemblage composition in urban areas, focusing on the role of taxonomic/functional *turnover* and/or *nestedness*, and how functional traits respond to urbanization. Spiders (Araneae) and carabids (Coleoptera, Carabidae) were selected as model groups, because of their well-defined ecology and taxonomy, together with their well-known response to urbanization, both in terms of taxonomic and functional diversity (e.g. Niemelä & Kotze, 2009; Sattler et al., 2010; Vergnes, Le Viol & Clergeau, 2012; Vergnes et al., 2014; Piano et al., 2017; Buchholz et al., 2018). The assemblages of the two selected groups were investigated by means of a hierarchical sampling design, combining data from isolated and connected control environmental patches along an urbanization gradient. The inner areas of traffic roundabouts were selected as isolated plots, while control patches were established on green areas connected with the surrounding environmental matrix. Specifically, we investigated whether: i) *nestedness* and *turnover* components differentially explain total variation (β -diversity) in taxonomic and functional diversity; ii) the urbanization level and patch isolation affect taxonomic and functional composition of carabid and spider communities, both in terms of homogenization (*nestedness*) and shift (*turnover*); and iii) functional traits show differential responses to the urbanization level and patch isolation.

Materials and methods

Sampling design

The study was carried out in 15 sampling plots (Fig. S1), randomly selected along an urbanization gradient in the municipality of Torino (about 880,000 inhabitants, NW-Italy). The average distance between the centre of sampling plots was 8,878 m (sd = $\pm 1,705.6$), ranging from 1,408 to 18,512 m. In order to test the effects of patch isolation on spiders and carabids, in each plot two sampling subplots were identified: i) one in an isolated patch, within a traffic roundabout; and ii) the other in the nearest green area, connected with the surrounding environmental matrix (connected control patch) (Fig. 1). Sampling plots consisted in circular areas of 150 m diameter (approximately 18,000 m²), centred on the roundabout. Roundabouts ranged from 6 to 30 m radius (i.e. approximately from 150 to 2,500 m² of surface area), and we evaluated

their age using historical aerial maps on Google Earth (<https://www.google.com/earth/download/ge/>). Based on the year of construction, we equally distributed them among three age classes (1 = less than 10 years; 2 = 10 years (built in 2007); 3 = more than 10 years) (see Appendix A: Table S1). Given that both taxonomic groups were not affected by these factors, namely the area and the age of the roundabouts, we did not include this information in our subsequent analyses. Connected control subplots were placed in the closest green area within the sampling plot, being represented by small green urban patches (1,000 m²), urban parks or seminatural areas at the city borders (up to a few hundreds of hectares). The isolated patch (roundabout) within a certain sampling plot was always smaller than the green area encompassing the connected control subplot. In all sampling plots, subplots were located in comparable semi-natural grassland habitats, maintained by regular mechanical mowing (see Fig. S2 for real examples). Roundabouts were assumed to represent a good approximation of isolated patches, since they are completely surrounded by roads, which likely constitute a selective barrier for our targeted arthropod groups. The urbanization level was assessed in each sampling plot by extrapolating the impervious surface coverage (ISA, Elvidge et al., 2007) from aerial images of the study area. We used the proportion (%) of impervious surfaces as a proxy for the urbanization level, which was calculated from updated digital maps (year 2017) by means of the QGIS software (QGIS Development Team, 2018) in a buffer of 1,600 m radius (see Fig. S1). We tried as much as possible to avoid overlapping buffer areas. However, due to logistic constraints related to permissions issued by the local authorities to access the areas of the roundabouts, our final design implied an overlap of 9.6 km² between buffer areas, corresponding to about 8% of the total area covered by the buffers (approximately 120 km²). Given that carabid beetles and spiders often respond to factors at different scales (Braaker et al., 2014; 2017), we checked whether this spatial scale represents the best option to evaluate the response of ground arthropods to urbanization in the investigated area (see Supplementary Materials).

Data collection

Ground-active arthropods were captured in each sampling subplot within a sampling section 30 m long using three pitfall traps (5-10 m apart), placed at least 20 cm from the patch border, and at least 5 m apart

to increase catch efficiency (Ward, New & Yen, 2001). Plastic jars (diameter 90 mm, length 110 mm) were dug into the ground so that the upper edge of the glass was flush with the soil surface, and filled with 20 ml of 50% propylene glycol solution. All traps were emptied every three weeks, in three sampling sessions between the 16th of May and the 18th of July 2017. The collected material was preserved in a 70% ethanol solution. Spiders and carabids were sorted, identified and counted in the laboratory according to the keys provided by Pesarini & Monzini (2010) and Boeken et al. (2002) for carabids, and by Nentwig et al. (2018) for spiders. Data from pitfall traps collected in the same subplot were pooled together for subsequent analyses.

It should be pointed out that pitfall traps provide data on activity density rather than real abundances of species, thus overestimating extremely active species. Although the pitfall trap-based sampling method introduces some bias in relative species abundances, the extent of the bias should be similar for each sampling site.

Functional traits

Body length, dispersal capacity and trophic requirements – hunting mode for spiders and trophic level for carabids – were considered as key functional traits, based on Buchholz et al. (2018).

Carabid species were assigned to two trophic groups (1 = zoophagous; 2 = phytophagous) according to Vanbergen et al. (2010), and to three dispersal groups based on wing development (1 = brachypterous; 2 = dimorphic; 3 = macropterous) according to Desender et al. (2008). The average body size was assigned to each species according to Desender et al. (2008). Spider species were assigned to functional groups reflecting their strategy of food provision, according to Cardoso et al. (2011). In order to obtain a comparable number of species among categories, we referred to a broader classification (1 = hunters; 2 = web-builders), without considering in detail the specific hunting strategies. Spiders were assigned to three dispersal groups (1 = non- or sporadic ballooning; 2 = ballooning at juvenile stages only; 3 = ballooning at juvenile and adult stages), based on Blandenier (2009), Bell et al. (2005) and Simonneau, Courtial and Pétillon (2016). Each species' male and female average body sizes were extrapolated from Nentwig et al.

(2018). We retained only female's data due to the high correlation between the two measures (Pearson's correlation test: $r = 0.97$; $P < 0.001$).

Data analysis

All statistical analyses were performed using the *R* software (R Core Team, 2017).

Preliminary Analyses. In order to identify the best scale of response to the urbanization level for carabids and spiders, we calculated the degree of urbanization for each station in three progressive larger buffers, defined as circles with a 100 m (small scale), 400 m (medium scale) and 1600 m (large scale) radius - with the roundabout as the centre. For each taxonomic group, we proceeded with fitting three separated models, one for each scale of the urbanization level, after eliminating outliers in our dependent variables following the standard protocol for data exploration proposed by Zuur et al. (2009). We tested the response of the total abundance of carabids and spiders against the urbanization level, patch isolation and their interaction by means of Generalized Linear Mixed Models (GLMMs) (Zuur et al. 2009), performed with the function "glmer.nb" in the *lme4* package (Bates et al., 2015). We assumed a negative binomial distribution after checking for the overdispersion of our dependent variables. To account for the spatial and temporal dependency, a station (*PlotID*) and a session identifier (*Session*) were incorporated as random factors in the models. We selected the one with the lowest AICc and, given that the best response was observed at the large scale (see Appendix B: Table S2), our subsequent analyses were performed using the urbanization level measured in the buffer of 1,600 m of radius. We then tested whether the total abundance of carabids and spiders in the isolated patch is influenced by the area and the age of the roundabout and by the distance of the roundabout from the control patch with the same model structure. No corrections to the data from the isolated patches were introduced to keep into account the effects of the area and the age of the roundabout and the distance between the roundabout and the control patch, since both groups were not affected by these factors (see Appendix B: Table S3).

Multivariate statistics. Firstly, we investigated the variation in taxonomic and functional composition in spider and carabid assemblages by calculating taxonomic and functional β -diversity across the study area. β -diversity was here intended as dissimilarity among samples and it was calculated by means of the

complement of the Sørensen index, which ranges from 0 (samples are composed exactly by the same species or functional groups) to 1 (samples do not share any species or functional groups). We used the function “beta” in the *BAT* package (Cardoso, Rigal & Carvalho, 2015), which returns the overall β -diversity and the contribution of its components, namely *turnover* and *nestedness*.

Secondly, we investigated the effects of the urbanization level and patch isolation on taxonomic and functional composition of both groups with multivariate statistics, performed with the *vegan* package (Oksanen et al., 2018). We first converted the urbanization level into a categorical variable by assigning sampling plots to one of three categories of urbanization: low (ISA < 50%), intermediate (ISA = 50-70%) and high (ISA > 70%). We then created a functional matrix, measuring the community-weighted means (CWM) of trait values with the function “functcomp” of the *FD* package (Laliberté & Legendre 2010; Laliberté, Legendre & Shipley, 2014). We built a site-by-trait matrix by multiplying the site-by-species matrix with a species-by-trait matrix resulting in the CWM trait values, which represent the mean trait value of all species in the community, weighted by their relative abundances, for body length (CWM-BL), dispersal (CWM-Disp) and trophic composition (CWM-Trophic). Increasing values in CWM-Trophic indicates a shift towards phytophagous species in carabids, and towards web-builders in spiders.

Taxonomic and functional composition among the three urbanization levels, and between control and isolated patches, were visualized by means of a Principal Coordinate Analysis (PCoA). We then tested whether the urbanization level and patch isolation were responsible for either taxonomic or functional homogenization by means of the Test of Homogeneity for Multivariate Dispersion (Anderson, Ellingsen & McArdle, 2006). This test measures the distance of each site to its associated group median calculated on a site-by-site distance matrix and subjects these values to an ANOVA (9,999 permutations) to assess if the variance differed among groups. For taxonomic diversity, the site-by-site distance matrix was computed on the matrix of relative abundance of species using the Bray-Curtis distance, whereas the Gower distance was applied to the CWM matrix to obtain the site-by-site distance matrix for functional diversity. To detect possible shifts in taxonomic and functional composition among urbanization and isolation levels, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001), specifying

urbanization, isolation and their interaction as factors. Statistical significance was tested via 9,999 random permutations with the sampling session (*Session*) and the ID of each sampling plot (*PlotID*) as strata.

To identify which taxa are specifically linked to the urbanization level and patch isolation categories, an Indicator Species Analysis was performed through the calculation of the *IndVal* (Indicator Value) index (Dufrêne & Legendre, 1997), using the function “multipatt” in the *indicspecies* package (De Caceres & Legendre, 2009).

Statistical models. The effects of the urbanization level, patch isolation and their interaction on community-averaged functional traits were tested with Generalized Linear Mixed Models (GLMMs) (Zuur et al., 2009), performed with the function “glmer” in the *lme4* package (Bates et al., 2015) assuming a normal error distribution. To account for the spatial and temporal dependency, a plot (*PlotID*) and a session identifier (*Session*) were incorporated as random factors in the models. The set of functional metrics employed in this analysis as dependent variables were extracted from the previously calculated functional matrices. In addition, in order to check for spatial autocorrelation, we calculated the observed Moran’s *I* for each model, comparing it with the expected values.

Results

A total of 215 out of 270 pitfall traps were retrieved during the whole sampling season. Overall, we collected a total of 1,722 carabids, belonging to 52 species, and 4,811 spiders, belonging to 66 species, with a mean of $5.28 \pm \text{sd} = 3.49$ (min = 4 and max = 13 species per subplot) and $6.86 \pm \text{sd} = 3.57$ (min = 1 and max = 19 species per subplot) species and $21.8 \pm \text{sd} = 22.4$ (min = 1; max = 126) and $34.9 \pm \text{sd} = 32.6$ (min = 3; max = 162) individuals per subplot respectively (see Appendix C: Tables S4-S5 for details on the recorded species of carabids; and Appendix D: Tables S6-S7 for details on the recorded species of spiders).

The pairwise dissimilarity (Fig. 2) among carabid communities (total β -diversity) within the sampling area, was on average higher for taxonomic ($0.84 \pm \text{sd} = 0.15$) than for functional diversity ($0.62 \pm \text{sd} = 0.12$). The contribution of the *nestedness* component to total β -diversity was higher than the *turnover* component in both taxonomic diversity (*turnover* = $0.34 \pm \text{sd} = 0.26$; *nestedness* = $0.51 \pm \text{sd} = 0.28$) and functional diversity

240 (*turnover* = $0.12 \pm \text{sd} = 0.21$; *nestedness* = $0.51 \pm \text{sd} = 0.28$). Similarly, total β -diversity was on average
 241 higher for taxonomic diversity ($0.77 \pm \text{sd} = 0.17$) than for functional diversity ($0.55 \pm \text{sd} = 0.21$) among
 242 spider communities within the sampling area and again the *nestedness* component showed a higher
 243 contribution than the *turnover* one for both taxonomic diversity (*turnover* = $0.32 \pm \text{sd} = 0.24$; *nestedness* =
 244 $0.44 \pm \text{sd} = 0.27$) and functional diversity (*turnover* = $0.10 \pm \text{sd} = 0.10$; *nestedness* = $0.44 \pm \text{sd} = 0.27$).
 245 The test of homogeneity for multivariate dispersion showed significant functional homogenization of both
 246 groups along the urbanization gradient (Table 1 and Fig. 3), whereas significant taxonomic homogenization
 247 was observed in isolated patches and urbanized plots for spiders (Table 1 and Fig. 4). The PERMANOVA
 248 revealed significant shifts in taxonomic and functional composition along the urbanization gradient for both
 249 groups. Spider taxonomic and functional composition was affected also by patch isolation and the
 250 interaction between urbanization and isolation, whereas carabid taxonomic composition showed a shift
 251 from connected to isolated patches (Table 2).
 252 The indicator species analysis highlighted no indicator species for urbanization categories in both groups.
 253 Some indicator species were identified for connected control subplots, namely *Harpalus serripes* (*IndVal* =
 254 0.562 ; $P = 0.001$) and *Harpalus tardus* (*IndVal* = 0.385 ; $P = 0.043$) for carabids; *Trochosa ruricola* (*IndVal* =
 255 0.549 ; $P = 0.008$), *Thanatus arenarius* (*IndVal* = 0.461 ; $P = 0.036$) and *Pardosa tenuipes* (*IndVal* = 0.366 ; $P =$
 256 0.049) for spiders. No indicator species were identified for isolated subplots.
 257 The response of carabid community-averaged functional traits revealed a significant increase of the
 258 proportion of phytophagous species with increasing urbanization level (range: 0.01-0.50), whereas no
 259 significant results were recorded for CWM-BL (body size) and CWM-Disp (Dispersal) (Table 3 and Fig. 5).
 260 Regarding spiders, body size was negatively affected by patch isolation, whereas the interaction term
 261 showed a significant positive effect, underlying that CWM-body size of spiders in isolated patches increases
 262 with increasing urbanization (Table 3). Both dispersal and trophic groups were significantly affected by all
 263 terms (Table 3). CWM-Disp (dispersal) showed an increasing trend along the urbanization gradient, ranging
 264 from 2.06 to 2.64, and higher values in the isolated ($2.26 \pm \text{sd} = 0.25$) than in the control ($2.16 \pm \text{sd} = 0.34$)
 265 subplots (Fig. 5), while the interaction factor displayed a negative effect. Regarding CWM-Trophic, the

relative proportion of web-builders significantly increased along the urbanization gradient (range = 0.27-0.82) and it was significantly higher in isolated ($0.68 \pm \text{sd} = 0.27$) than in control ($0.69 \pm \text{sd} = 0.30$) subplots, while a negative effect was observed for the interaction factor (Fig. 5).

Lastly, Moran's I revealed that CWM-Disp and CWM-Trophic, but not CWM-BL, of both carabids and spiders show significant spatial autocorrelation (Table 4).

Discussion

In this work, we analyzed how urbanization and fragmentation drive the *turnover* and *nestedness* patterns of taxonomic and functional diversity within two taxonomic groups of ground arthropods, namely carabids and spiders. Since we consistently sampled the same habitat type (i.e. semi-natural grasslands) exposed to the same management practices, we could clearly depict the effect of site location within the conurbation, without confounding factors due to local habitat characteristics.

Our results showed that taxonomic variation was higher than functional variation within both carabid and spider communities along the urbanization and isolation gradients. This is in accordance with the functional redundancy concept (Lawton & Brown, 1993) stating that multiple species perform similar roles in communities and ecosystems (e.g. Petchey et al., 2007). This would guarantee high ecological resilience to disturbance, which is particularly crucial for the maintenance of ecosystem functions in extremely altered habitats, like urban areas. Decomposing β -diversity into its components revealed that the same mechanisms drive variation in taxonomic and functional composition in the two taxa studied. Since *nestedness* was the dominant component, some sampling plots host a subset of species of other sites. We can hypothesize that both carabid and spider communities are composed of both specialized species, surviving only in few localities, and generalist species, which can exploit a broad range of ecological conditions. In the same way, some functional traits are removed from some sites without being replaced, with possible repercussions on ecosystem functionality.

Results of the test of homogeneity for multivariate dispersion showed that spiders were more affected by the urbanization level and patch isolation than carabids. Taxonomic homogenization (i.e. *nestedness*) was

observed only in spiders and it was explained by both the urbanization level and patch isolation. In addition, the role of isolation as a driver of taxonomic homogenization was further confirmed by the indicator species analysis that revealed indicator species for connected control subplots only. According to these results, we may hypothesize that connected control subplots could provide source populations for the isolated ones, guaranteeing their survival in disturbed habitats, likely recalling the island biogeographic model in fragmented landscapes (MacArthur & Wilson, 1967; Leibold & Chase, 2017). However, no indicator species were identified for the urbanization categories. Indicator species may not have been detected because they are too scarce and irregularly distributed among the subplots within each category. This result may however suggest that the observed *nestedness* pattern along the urbanization gradient may be due to varying relative abundances, instead of an effective substitution of species.

Regarding functional composition, the urbanization level causes functional homogenization in both communities. This may be due mainly to a filtering process, supporting the hypothesis that urbanization alters the functional community composition by shifting species composition towards more functionally homogeneous assemblages. Conversely, patch isolation did not significantly affect the functional composition of both carabid and spider communities, underpinning how the urbanization level alone may explain functional variation among samples. This corroborates the hypothesis that stochastic events, like dispersal-related processes or ecological drift, determine species richness in isolated patches for both carabids and spiders (Chase & Myers, 2011; Leibold & Chase, 2017). These outcomes parallel Concepción et al. (2017) who found functional homogenization with increasing urbanization in vascular plants and birds. On the contrary, our results are in contrast with those reported by Brice, Pellerin and Poulin (2017), who observed both taxonomic and functional differentiation with increasing urbanization in plant communities. These contrasting results are likely due to the fact that plant diversity often increases in urban habitats because of the unique abiotic conditions and disturbance regimes, favoring exotic species (McKinney, 2008). In our case, we did not record any exotic species in the examined communities, thus, at least from this point of view, our results seem to reflect the filtering effect of urbanization without confounding factors. However, increasing differentiation might also emerge from differential human activities in urban

green spaces, facilitating certain species in some places or eliminating others elsewhere. This could have also happened in our case with spiders and carabid beetles, which could be easily transported in the soil or in plant pots as eggs, juvenile stages or even as adults.

The results of the PERMANOVA performed on taxonomic composition pointed out a combined effect of the urbanization level and patch isolation on the taxonomic shift—i.e. *turnover* component in both taxonomic groups. The role of urbanization as a driver of this process has already been pointed out by Knop (2016) for canopy insects, who observed true species replacement in terms of relative abundances in three insect groups, including ground beetles, when comparing rural against urban areas. Regarding functional composition, urbanization caused a shift in both examined groups, whereas patch isolation affected only spiders, and these trends are confirmed by the analysis of the response of functional traits.

Dispersal capacity significantly increased along the urbanization gradient for spiders. In particular, this increasing trend was clear in connected control subplots, while isolated subplots hosted highly dispersive species, regardless of the urbanization level. High dispersal capacity is essential in disturbed habitats in order to escape adverse environmental conditions and to enhance population survival in the area; vice-versa in stable, late-successional habitats more energy can be invested in reproduction, favoring the establishment of less dispersive species (Roff, 1975). Hence, the observed decline in low-dispersive species appears in accordance with the dynamic nature of urban environments, where human activities result in high turnover rates of suitable habitat patches (Parris, 2016). The observed high dispersal capacity of spiders in isolated subplots can be explained in the framework of the theory of island biogeography (MacArthur & Wilson, 1967), which predicts that isolation of suitable patches increases extinction rates. Therefore, only highly dispersive species can support viable populations in isolated patches, due to the continuous immigration of new individuals, increasing the average dispersal capacity of the community.

Surprisingly, we did not record any effect of the urbanization level or patch isolation on carabid dispersal capacity, in contrast with the available literature (Piano et al., 2017). The differential response obtained for the two examined arthropod groups might be due to their different dispersal mode, i.e. active dispersal in carabids and passive dispersal in spiders. The peculiar dispersal mode of spiders, i.e. ballooning, requires

particular physical conditions to occur (Weyman, 1993; Simonneau, Courtial & Pétilon, 2016) and dispersing individuals have no control over the flight direction (Compton, 2002). In heavily fragmented landscapes, the probability to reach isolated patches is therefore strictly related to the ballooning performance, which is maximized in highly dispersive species (Bonte et al., 2003). Conversely, carabid dispersal, either cursorial or by flight, is active and not constrained by the physical environment, therefore all species likely have the same probability to reach isolated patches.

The analysis of the trophic structure revealed how urbanization strongly acts on both examined taxa. Regarding carabids, we observed a significant replacement of zoophagous with phytophagous species. Phytophagous carabids are specialized on seeds from ruderal plants (Thiele, 1977; Honek et al. 2007; Honek, Martinkova & Saska, 2011), which typically occur in highly impermanent sites (Ribera et al., 2001). Phytophagous species can therefore be considered adapted to ruderal habitats (Vanbergen et al., 2010), likely supporting viable populations within urban sites in our study. Concerning spiders, the proportion of web-builders significantly increases with increasing the urbanization level in connected control subplots. Conversely, in isolated subplots, web-builder proportion is higher than connected control subplots regardless of the urbanization level, suggesting how the effect of patch isolation overrides urbanization in determining the trophic structure of spiders. This may be due to the fact that patch isolation may negatively affect preys of cursorial spiders (Hawn et al., 2018) with consequent negative effects on hunters (Gravel et al., 2011; Zalewski et al., 2018). However, it should be pointed out that this shift from hunters to web-builders in isolated patches might also be a consequence of the dispersal-based selection, since, in our study, web-builders include most of the highly dispersive species (i.e. linyphiids).

Contrary to our expectations, body size did not respond to the urbanization gradient in our study for both taxonomic groups, in accordance with Buchholtz et al. (2018). However, we observed a significant decrease of spider body size along the urbanization gradient in connected control patches, but not in isolated ones. It has been demonstrated that community-wide body-size shifts occur in urban communities as a consequence of increased temperatures due to the urban heat-island effect, but these shifts are mediated by the dispersal capacity of each taxon (Merckx et al., 2018). Thus, this lack of response may result from the

dispersal-mediated effect, since higher dispersal capacity of spider species recorded in roundabouts may dampen the urban heat-island effect on body size.

Results of the Moran's I test revealed that there is high spatial autocorrelation among sampling plots in terms of dispersal capacity and trophic composition, but not of body size, for both groups. These patterns underlie the role of the spatial arrangement of individuals in a landscape, which is rarely random (McGlinn et al., 2019). Instead, most individuals are spatially clustered or aggregated in some way, with repercussions also on the functional traits, as demonstrated by our results.

Conclusions

Overall, we here highlighted differential mechanisms underlying the selective pressure exerted by urbanization and fragmentation on ground arthropods, showing a more evident response in spiders than carabids. This is in accordance with literature, which highlighted how top predators are usually more sensitive to urbanization than lower trophic levels (Egerer et al., 2017; El-Sabawii, 2018).

We have demonstrated that *nestedness* more than *turnover* explains taxonomic and functional variation in the examined communities, indicating a loss of species and functionality among sampling plots. This homogenization process is mainly due to urbanization, which filters species based on their functional traits in both the examined groups.

In addition, the high spatial autocorrelation among sampling plots identified for dispersal capacity and trophic composition underlies that stochastic factors, e.g. source-sink dynamics, also play a role in driving the functional composition of examined communities. Stochastic events, like those caused by human activities, may cause the extinction of some species in the examined sampling plots, potentially compromising the species survival in the whole sampling area. This may have repercussions on ecosystem functionality if key stone species are removed from the landscape.

Our approach, thus, proved to be particularly useful to understand how different facets of urbanization affect biodiversity, providing a valuable framework to predict how biotic communities will respond to increasing anthropogenic pressures associated with urbanization. In the next future, further investigations

should be performed to highlight alterations at the ecosystem level in order to provide management suggestions aiming at reducing negative effects caused by urbanization.

Acknowledgement

We thank Giulia Chiampo and Simone Savio for their help in the field work and in sample sorting, and Giovanni Allegro for checking identifications of carabid species. Alexandra Jones is greatly acknowledged for her linguistic revision. The authors declare no conflicts of interest.

Funding

This work is part of the research fellowship “Bando dei Talenti della Società Civile 2016” funded by the Fondazione Gorla, the University of Turin and the Royal Belgian Institute of Natural Sciences.

Appendix A. Supplementary data

Appendix B. Supplementary data

Appendix C. Supplementary data

Appendix D. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX

References

- Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32-46.
- Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9(6), 683-693.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1-48.
- Bell, J. R., Bohan, D. A., Shaw, E. M., & Weyman, G. S. (2005). Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research*, 95(2), 69-114.
- Blandenier, G. (2009). Ballooning of spiders (Araneae) in Switzerland: general results from an eleven-year survey. *Arachnology*, 14(7), 308-316.
- Boeken, M., Desender, K., Drost, B., van Gijzen, T., Koese, B., Muilwijk, J., Turin, H., & Vermeulen, R. (2002). *De Loopkevers van Nederland en Vlaanderen (Coleoptera: Carabidae)*. Stichting Jeugdbondsuitgeverij, Utrecht.
- Bonte, D., Vandenbroecke, N., Lens, L., & Maelfait, J. P. (2003). Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1524), 1601-1607.
- Braaker, S., Ghazoul, J., Obrist, M. K., & Moretti, M. (2014). Habitat connectivity shapes urban arthropod communities: the key role of green roofs. *Ecology*, 95(4), 1010-1021.
- Braaker, S., Obrist, M. K., Ghazoul, J., & Moretti, M. (2017). Habitat connectivity and local conditions shape taxonomic and functional diversity of arthropods on green roofs. *Journal of Animal Ecology*, 86(3), 521-531.
- Brice, M. H., Pellerin, S., & Poulin, M. (2017). Does urbanization lead to taxonomic and functional homogenization in riparian forests?. *Diversity and Distributions*, 23(7), 828-840.

436 Buchholz, S., Hannig, K., Möller, M., & Schirmel, J. (2018). Reducing management intensity and isolation as
 437 promising tools to enhance ground-dwelling arthropod diversity in urban grasslands. *Urban ecosystems*,
 438 21(6), 1139-1149.

439 Cardoso, P., Pekár, S., Jocqué, R., & Coddington, J. A. (2011). Global patterns of guild composition and
 440 functional diversity of spiders. *PloS one*, 6(6), e21710.

441 Cardoso, P., Rigal, F., & Carvalho, J. C. (2015). BAT—Biodiversity Assessment Tools, an R package for the
 442 measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in*
 443 *Ecology and Evolution*, 6(2), 232-236.

444 Chace, J. F., & Walsh, J. J. (2006). Urban effects on native avifauna: a review. *Landscape and Urban*
 445 *Planning*, 74(1), 46-69.

446 Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic
 447 processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1576),
 448 2351-2363.

449 Compton, S. G. (2002). Sailing with the wind: dispersal by small flying insects. In *Dispersal ecology* (ed. J. M.
 450 Bullock, R. E. Kenward & R. S. Hails), pp. 113–133. Oxford: British Ecological Society, Blackwell Scientific.

451 Concepción, E. D., Moretti, M., Altermatt, F., Nobis, M. P., & Obrist, M. K. (2015). Impacts of urbanization
 452 on biodiversity: the role of species mobility, degree of specialisation and spatial scale. *Oikos*, 124, 1571-
 453 1582.

454 Concepción, E. D., Götzenberger, L., Nobis, M. P., de Bello, F., Obrist, M. K., & Moretti, M. (2017).
 455 Contrasting trait assembly patterns in plant and bird communities along environmental and human-induced
 456 land-use gradients. *Ecography*, 40(6), 753-763.

457 De Caceres, M., Legendre, P. (2009). Associations between species and groups of sites: indices and
 458 statistical inference. *Ecology*, URL <http://sites.google.com/site/miqueldecaceres/>

459 Desender, K., Dekoninck, W., Maes, D. M. M. V., Crevecoeur, L., Dufrêne, M., Jacobs, M., Lambrechts, J.,
 460 Pollet, M., Stassen, E., & Thys, N. (2008). Een nieuwe verspreidingsatlas van de loopkevers en
 461 zandloopkevers (Carabidae) in België. Rapporten van het Instituut voor Natuur- en Bosonderzoek 2008
 462 (INBO.R.2008.13). Instituut voor Natuur- en Bosonderzoek, Brussel.

463 Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible
 464 asymmetrical approach. *Ecological Monographs*, 67(3), 345-366.

465 Egerer, M. H., Arel, C., Otoshi, M. D., Quistberg, R. D., Bichier, P., & Philpott, S. M. (2017). Urban arthropods
 466 respond variably to changes in landscape context and spatial scale. *Journal of Urban Ecology*, 3.

467 El-Sabaawi, R. (2018). Trophic structure in a rapidly urbanizing planet. *Functional Ecology*, 32, 1718–1728.

468 Elvidge, C.D., Tuttle, B.T., Sutton, P.C., Baugh, K.E., Howard, A.T., Milesi, C., Bhadura, B.L., & Nemani, R.,
 469 (2007). Global distribution and density of constructed impervious surfaces. *Sensors*, 7, 1962e1979.

470 Gianuca, A. T., Engelen, J., Brans, K. I., Hanashiro, F. T., Vanhamel, M., Van den Berg, E. M., Souffreau, C., &
 471 De Meester, L. (2018). Taxonomic, functional and phylogenetic metacommunity ecology of cladoceran
 472 zooplankton along urbanization gradients. *Ecography*, 41(1), 183-194.

473 Gravel, D., Massol, F., Canard, E., Mouillot, D. & Mouquet, N. (2011). Trophic theory of island biogeography.
 474 *Ecology Letters* 14, 1010–1016.

475 Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2006). Global
 476 change and the ecology of cities. *Science*, 319, 756-760.

477 Hawn, C. L., Herrmann, J. D., Griffin, S. R., & Haddad, N. M. (2018). Connectivity increases trophic subsidies
 478 in fragmented landscapes. *Ecology Letters*, 21(11), 1620-1628.

479 Honek, A., Martinkova, Z., Saska, P., & Pekar, S. (2007). Size and taxonomic constraints determine the seed
 480 preferences of Carabidae (Coleoptera). *Basic and Applied Ecology*, 8(4), 343-353.

481 Honek, A., Martinkova, Z., & Saska, P. (2011). Effect of size, taxonomic affiliation and geographic origin of
 482 dandelion (*Taraxacum* agg.) seeds on predation by ground beetles (Carabidae, Coleoptera). *Basic and*
 483 *Applied Ecology*, 12(1), 89-96.

484 Jones, E. L., & Leather, S. R. (2013). Invertebrates in urban areas: a review. *European Journal of*
 485 *Entomology*, 109(4), 463-478.

486 Knop, E. (2016). Biotic homogenization of three insect groups due to urbanization. *Global Change Biology*,
 487 22, 228-236.

488 Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from
 489 multiple traits. *Ecology*, 91, 299-305.

490 Laliberté, E., Legendre, P., & Shipley, B. (2014). FD: measuring functional diversity from multiple traits, and
 491 other tools for functional ecology. R package version 1.0-12.

492 La Sorte, F. A., Aronson, M. F., Williams, N. S., Celesti-Grapow, L., Cilliers, S., Clarkson, B. D., Dolan, R. W.,
 493 Hipp, A., Klotz, S., Kühn, I., Pyšek, P., Siebert, S., & Winter, M. (2014). Beta diversity of urban floras among
 494 European and non-European cities. *Global Ecology and Biogeography*, 23(7), 769-779.

495 Lawton, J. H., & Brown, V. K. (1993). Redundancy in ecosystems. – In: Schulze, E.-D., & Mooney, H. A. (eds),
 496 *Biodiversity and ecosystem function*. Springer, pp. 255–270.

497 Legendre, P., & Legendre, L. (1998). *Numerical Ecology*, Volume 24. *Developments in Environmental*
 498 *Modelling*.

499 Leibold, M.A., Chase, J.M., (2017). *Metacommunity Ecology – Monographs in Population Biology*, Volume
 500 59. Princeton University Press, 504 pp.

501 Luck, G. W., & Smallbone, L. T. (2010). Species diversity and urbanization: patterns, drivers and
 502 implications. *Urban Ecology*, 88-119.

503 MacArthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press,
504 Princeton.

505 McDonnell, M. J., & Hahs, A. K. (2008). The use of gradient analysis studies in advancing our understanding
506 of the ecology of urbanizing landscapes: current status and future directions. *Landscape Ecology*, 23, 1143-
507 1155.

508 McGlinn, D. J., Xiao, X., May, F., Gotelli, N. J., Engel, T., Blowes, S. A., Knight, T., Purschke, O., Chase, J.,
509 McGill, B. J. (2019). MoB (Measurement of Biodiversity): a method to separate the scale-dependent effects
510 of species abundance distribution, density, and aggregation on diversity change. *Methods in Ecology and*
511 *Evolution*, 10(2), 258-269.

512 McKinney, M. L. (2002). Urbanization, Biodiversity and Conservation. *BioScience*, 52(10), 883-890.

513 McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*,
514 127, 247-260.

515 McKinney, M. L. (2008). Effects of urbanization of species richness: a review of plants and animals. *Urban*
516 *Ecosystems*, 11, 161-176.

517 Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L. F., Backeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel,
518 M., Debortoli, N., De Wolf, K., Engelen, J. M. T., Fontaneto, D., Gianuca, A. T., Govaert, L., Hendrickx, F.,
519 Higuti, J., Lens, L., Martens, K., Matheve, H., Matthysen, E., Piano, E., Sablon, R., Schön, I., Van Donink, K.,
520 De Meester, L., & Van Dyck, H. (2018a). Body-size shifts in aquatic and terrestrial urban communities.
521 *Nature*, 558(7708), 113.

522 Nentwig, W., Blick, T., Gloor, D., Hänggi, A., & Kropf, C. (2018). Version December.2018. Online at
523 <https://www.araneae.nmbe.ch>, accessed on December 2018. doi: 10.24436/1

524 Niemelä, J., & Kotze, D. J. (2009). Carabid beetle assemblages along urban to rural gradients: A review.
525 *Landscape and Urban Planning*, 92, 65-71.

526 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H.
 527 H., & Wagner, H. (2018). *vegan: Community Ecology Package*. R package version 2.2-1. [http://CRAN.R-](http://CRAN.R-project.org/package=vegan)
 528 [project.org/package=vegan](http://CRAN.R-project.org/package=vegan).
 529 Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary
 530 consequences of biotic homogenization. *Trends in Ecology & Evolution*, 19(1), 18-24.
 531 Parris, K. M. (2016). *Ecology of Urban Environments*. Wiley-Blackwell, Chichester, West Sussex, UK.
 532 Pesarini, C., & Monzini, V. (2010). *Insetti della fauna italiana – Coleotteri Carabidi vol. I e II*. Museo di Storia
 533 Naturale di Milano, 296 pp.
 534 Petchey, O. L., Evans, K. L., Fishburn, I. S., & Gaston, K. J. (2007). Low functional diversity and no
 535 redundancy in British avian assemblages. *Journal of Animal Ecology*, 76(5), 977-985.
 536 Pickett, S. T., Cadenasso, M. L., Grove, J. M., Boone, C. G., Groffman, P. M., Irwin, E., Kaushal, S. S., Marshall,
 537 V., McGrath, B. P., Nilon, C. H., Pouyat, R. V., Szlavecz, K., Troy, A., & Warren, P. (2011). Urban ecological
 538 systems: Scientific foundations and a decade of progress. *Journal of Environmental Management*, 92(3),
 539 331-362.
 540 Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D. E., Isaia, M., Lens, L., Merckx, T., Mertens, D., van
 541 Kerckvoorde, M., De Meester, L., & Hendrickx F. (2017). Urbanization drives community shifts towards
 542 thermophilic and dispersive species at local and landscape scales. *Global Change Biology*, 23(7), 2554-2564.
 543 Piano, E., Souffreau, C., Merckx, T., Baardsen, L. F., Backeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel,
 544 M., Debortoli, N., Decaestecker, E., De Wolf, K., Engelen, J. M. T., Fontaneto, D., Gianuca, A. T., Govaert, L.,
 545 Hanashiro, F. T. T., Higuti, J., Lens, L., Martens, K., Matheve, H., Matthysen, E., Pinseel, E., Sablon, R., Schon,
 546 I., Stocks, R., Van Doninck, K., Van Dyck, H., Vanormelingen, P., Van Wichelen, J., Vyverman, W., De
 547 Meester, L., Hendrickx, F. (2019). Urbanization drives cross-taxon declines in abundance and diversity at
 548 multiple spatial scales. *Global Change Biology*, <https://doi.org/10.1111/gcb.14934>.

549 QGIS Development Team (2018). QGIS Geographic Information System. Open Source Geospatial
550 Foundation Project. <http://qgis.osgeo.org>

551 R Development Core Team (2017). R: A language and environment for statistical computing. R Foundation
552 for Statistical Computing, Vienna, Austria. <http://www.R-project.org>

553 Ramírez-Restrepo, L., & MacGregor-Fors, I. (2017). Butterflies in the city: a review of urban diurnal
554 Lepidoptera. *Urban Ecosystems*, 20(1), 171-182.

555 Rebele, F. (1994). Ecology and special features of urban ecosystems. *Global Ecology and Biogeography*
556 *Letters*, 4, 173–187.

557 Ribera, I., Dolédec, S., Downie, I. S., & Foster, G. N. (2001). Effect of land disturbance and stress on species
558 traits of ground beetle assemblages. *Ecology*, 82(4), 1112-1129.

559 Roff, D. A. (1975). Population stability and the evolution of dispersal in a heterogeneous environment.
560 *Oecologia*, 19, 217–237.

561 Sattler, T., Borcard, D., Arlettaz, R., Bontadina, F., Legendre, P., Obrist, M. K., & Moretti, M. (2010). Spider,
562 bee, and bird communities in cities are shaped by environmental control and high stochasticity. *Ecology*,
563 91(11), 3343-3353.

564 Seto, K. C., Fragkias, M., Güneralp, B., & Reilly, M. K. (2011). A meta-analysis of global urban land
565 expansion. *PLoS ONE*, 6(8), e23777.

566 Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., & Hope, D. (2006). From patterns to emerging
567 processes in mechanistic urban ecology. *Trends in Ecology and Evolution*, 21(4), 186-191.

568 Shochat, E., Lerman, S. B., Anderies, J. M., Warren, P. S., Faeth, S. H., Nilon, C. H. (2010). Invasion,
569 competition, and biodiversity loss in urban ecosystems. *BioScience*, 60(3), 199-208.

570 Simonneau, M., Courtial, C., & Pétilon, J. (2016). Phenological and meteorological determinants of spider
571 ballooning in an agricultural landscape. *Comptes Rendus Biologies*, 339(9-10), 408-416.

572 Small, E., Sadler, J. P., & Telfer, M. (2006). Do landscape factors affect brownfield carabid assemblages?
 573 Science of the Total Environment, 360, 205–222.

574 Southwood, T. R. E. (1977). Habitat, the templet for ecological strategies?. Journal of Animal Ecology, 337-
 575 365.

576 Southwood, T. R. E. (1988). Tactics, strategies and templets. Oikos, 52(1), 3-18.

577 Thiele, H. U. (1977). Carabid Beetles in Their Environments: A Study on Habit Selection by Adaptations in
 578 Physiology and Behaviour. Translated by Joy Wieser. Springer-Verlag.

579 Turrini, T., & Knop, E. (2015). A landscape ecology approach identifies important drivers of urban
 580 biodiversity. Global Change Biology, 21(4), 1652-1667.

581 Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer's guide to nestedness analysis. Oikos,
 582 118(1), 3-17.

583 Vanbergen, A. J., Woodcock, B. A., Koivula, M., Niemelä, J., Kotze, D. J., Bolger, T., Golden, V., Dubs, F.,
 584 Boulanger, G., Serrano, J., Lencina, J. L., Serrano, A., Aguiar, C., Grandchamp, A-C., Stofer, S., Szél, G., Ivits,
 585 E., Adler, P., Markus, J., & Watt, A. D. (2010). Trophic level modulates carabid beetle responses to habitat
 586 and landscape structure: a pan-European study. Ecological Entomology, 35(2), 226-235.

587 Vergnes, A., Le Viol, I., & Clergeau, P. (2012). Green corridors in urban landscapes affect the arthropod
 588 communities of domestic gardens. Biological Conservation, 145(1), 171-178.

589 Vergnes, A., Pellissier, V., Lemperiere, G., Rollard, C., & Clergau, P. (2014). Urban densification causes the
 590 decline of ground-dwelling arthropods. Biodiversity and Conservation, 23, 1859-1877.

591 Ward, D. F., New, T. R., & Yen, A. L. (2001). Effects of pitfall trap spacing on the abundance, richness and
 592 composition of invertebrate catches. Journal of Insect Conservation, 5(1), 47-53.

593 Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I., & LeRoy Poff, N. (2010). A structured and dynamic
 594 framework to advance trait-based theory and prediction in ecology. Ecology Letters, 13, 267-283.

- 595 Weyman, G.S. (1993). A review of the possible causative factors and significance of ballooning in spiders.
596 *Ethology, Ecology and Evolution*, 5(3), 279-291.
- 597 Zalewski, M., Hajdamowicz, I., Stańska, M., Dudek-Godeau, D., Tykarski, P., Sienkiewicz, P., Ciurzycki, W., &
598 Ulrich, W. (2018). β -diversity decreases with increasing trophic rank in plant–arthropod food chains on lake
599 islands. *Scientific Reports*, 8, 17425.
- 600 Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions*
601 *in ecology with R*. Springer Science & Business Media.

FIGURE CAPTIONS

Fig. 1. Schematic representation of the nested sampling design adopted in this research. Sampling plots were placed along an urbanization gradient, each one being composed of two subplots (I = isolated; C = connected control). In each sub-plot, three pitfall traps were activated during the sampling period (black dots).

Fig. 2. Barplot representing the contribution of *turnover* (dark grey) and *nestedness* (light grey) to the total taxonomic and functional β -diversity for carabids (left panel) and spiders (right panel).

Fig. 3. Ordination of carabid (left) and spider (right) communities, according to the first two PCoA axes performed on taxonomic (upper panel) and functional (lower panel) composition. Ellipses represent standard deviations around the medians of urbanization levels (green = low; orange = intermediate; purple = high). Different symbols represent sampling subplots belonging to different urbanization levels (circles = low; squares = intermediate; triangles = high). The animal silhouettes are from PhyloPic (<http://www.phylopic.org>).

Fig. 4. Ordination of carabid (left) and spider (right) communities, according to the first two PCoA axes performed on taxonomic (upper panel) and functional (lower panel) composition. Ellipses represent standard deviations around the medians of isolation levels (blue = connected control; brown = isolated). Different symbols represent sampling subplots belonging to different isolation categories (circles = connected control; squares = isolated). The animal silhouettes are from PhyloPic (<http://www.phylopic.org>).

Fig. 5. Predicted CWM values (CWM-Trophic = trophic composition; CWM-BL = body length; CWM-Disp = dispersal) and confidence intervals along the urbanization gradient for carabids and spiders (light blue line = connected control patch data; orange line = isolated patch data). Only significant trends are reported. The animal silhouettes are from PhyloPic (<http://www.phylopic.org>).

Figure 1

[Click here to access/download;Figure;Fig1_new.jpg](#)

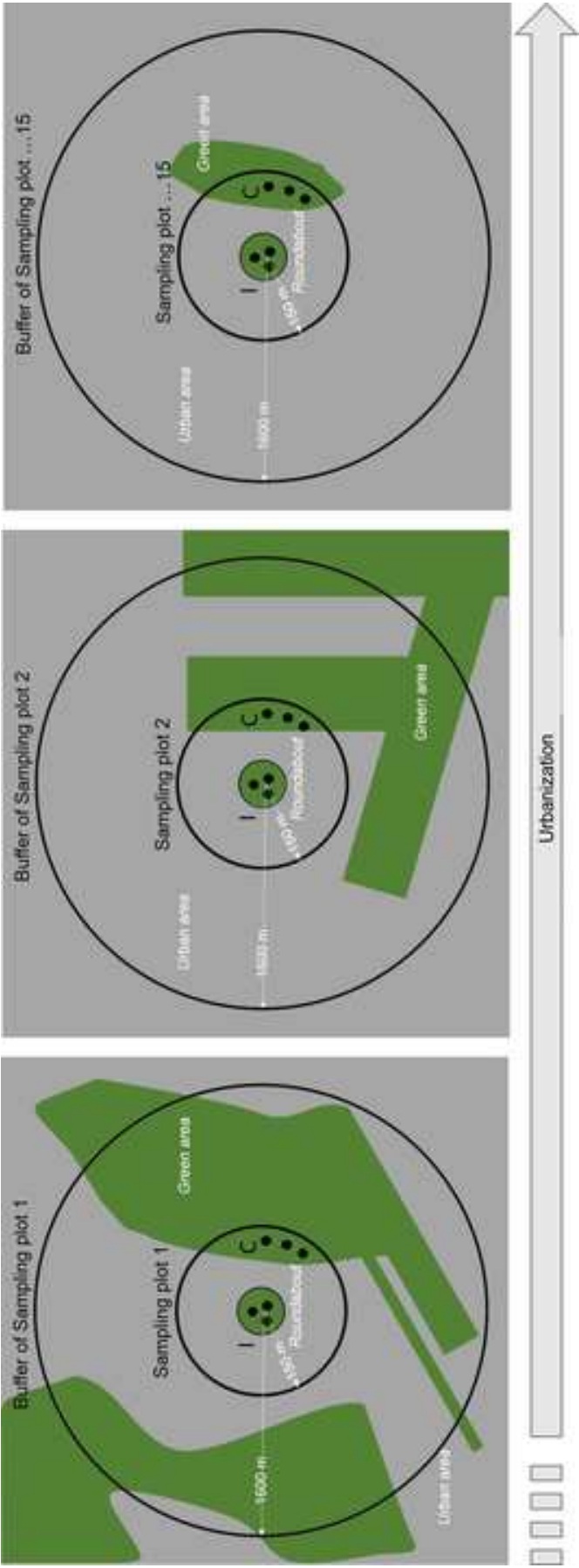


Figure 5

[Click here to access/download;Figure;Fig_5_new.tif](#)

